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Volume XXXI - Fascicolo I

STEFANIA NOSOTTI & OLIVIER RIEPPEL

THE BRAINCASE OF *PLACODUS* AGASSIZ, 1833 (REPTILIA, PLACODONTIA)

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In copertina: ricostruzione del cranio di *Placodus*. Disegno di Massimo Demma.

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The braincase of *Placodus* Agassiz, 1833 (Reptilia, Placodontia)

Abstract - The braincase of *Placodus* is described on the basis of all available specimens that preserve the relevant structures. Particular emphasis is placed on the interpretation of the "alisphenoid bridge" and the sphenoid region. Competing alternative interpretations of the neurocranial ossifications are attempted that match the structure of the braincase with the structure of the brain, known from two endocasts. The various skulls available document profound variation in the sphenoid region, and the methodological implications of this are briefly considered.

Key-words - *Placodus*, braincase, neurocranium, "alisphenoid bridge", hypophysis.

Riassunto - La scatola cranica di *Placodus* Agassiz, 1833 (Reptilia, Placodontia).

Nel presente lavoro è descritta la morfologia della scatola cranica di *Placodus* sulla base di esemplari che espongono anche le strutture endocraniche (neurocranio). Particolarmente problematica si è rivelata l'interpretazione della regione sfenoidale e del cosiddetto "ponte alisfenoidale", ossificazione impari che collega dorsalmente i processi clinoidei del basisfenoide. Tali difficoltà interpretative scaturiscono dalla variabilità della morfologia della base cranica nei diversi esemplari esaminati - variabilità cui gli autori non attribuiscono un significato tassonomico - e dalla posizione del "ponte alisfenoidale" relativa alle strutture della base cranica. Queste caratteristiche del materiale in studio rendono estremamente problematica un'interpretazione della morfologia che si accordi in modo pienamente soddisfacente con la presunta struttura dell'encefalo. Si propongono due ipotesi alternative, la più plausibile delle quali risulta nell'interpretazione del "ponte alisfenoidale" come una struttura neomorfica posizionata nella plica ventralis, dunque postero-ventralmente all'infundibulum. Corollario di questa interpretazione è che l'ipofisi sarebbe localizzata in una posizione molto anteriore rispetto al dorsum sellae, con un'estensione anteriore dell'infundibulum che non ha riscontro in altri rettili. Si sottolinea quindi che nessuna delle due ipotesi proposte consente un'interpretazione pienamente coerente dei dati a disposizione. Viene infine brevemente discusso l'approccio metodologico allo studio di questo tipo di materiale.

Parole chiave - *Placodus*, scatola cranica, neurocranio, "ponte alisfenoidale", ipofisi.

INTRODUCTION

The systematics, morphology, paleobiogeography and paleobiology of the genus *Placodus* Agassiz, 1833 was recently reviewed by Rieppel (1995). In describing the anatomy of the skull of *Placodus*, Rieppel (1995) commented on findings of earlier authors, and presented an up-to-date synthesis of the knowledge then available. Rieppel (1995) did not describe the braincase of *Placodus* in any detail, however, but only briefly discussed the morphological relations of the ossified elements of the neurocranium, and how these relate to the ossifications in the palatoquadrate (epipterygoid, quadrate) and associated dermatocranial elements (palatine and pterygoid), cursorily touching upon the course of the internal carotids, and on the facialis and trigeminal nerves.

Re-examination of the acid-prepared specimen BT 13 from the Oberfränkisches Erdgeschichtliches Museum in Bayreuth, and the comparison of the latter with the *Placodus* material kept at the Senckenberg Museum in Frankfurt a.M., especially the skull described by Broili (1912), permits the authors of the present contribution to present a more accurate and more detailed description of the braincase of *Placodus*, in particular of the neurocranium, and a different interpretation of some details of the skull anatomy of *Placodus* in general. It should be noted however, that collectively this material documents an unusual degree of plasticity in the sphenoid region of the skull of *Placodus*. The nature of this plasticity is difficult to assess, but we assume in this paper that it is due to individual (ontogenetic?) rather than taxonomic variation. It is in part due to that plasticity that an unequivocal interpretation of all aspects of the braincase structure remains elusive. Whereas the main goal of this paper is the description and discussion of the braincase of *Placodus*, refined illustrations of the overall skull morphology of the genus are presented in Figures 1A, B - 6A, B.

LIST OF ABBREVIATIONS

ab	"alisphenoid bridge"
af	abducens nerve foramen
ap	ascending process
app	ascending process of the palatine
bo	basioccipital
bot	basioccipital tuber
bp	basipterygoid process
bs + ps	para-basisphenoid
ccf	foramina for the cerebral branches of the internal carotids (= cerebral carotid foramina)
ch	cartilago hypochiasmatica
cp	clinoid process of the basisphenoid
df	dental foramen (dental lamina foramen)
ds	dorsum sellae
e	epipterygoid
ect	ectopterygoid
eo	exoccipital
f	frontal
fm	foramen magnum
Fv	fenestra vestibuli
hyf	hypoglossal nerve foramen
hyp	hypophyseal pit
ic	presumed route of the internal carotid
j	jugal
jf	jugular foramen
m	maxilla
n	nasal
op	opisthotic
p	parietal
pf	postfrontal
pF	prootic fenestra
pfo	parietal foramen
pit	restored pituitary fossa
pl	palatine
pm	premaxilla
po	postorbital
pp	paroccipital process of the opisthotic
pr	prootic
prf	prefrontal
pt	pterygoid
ptF	post-temporal fenestra
q	quadrate
sc	sagittal crest
so	supraoccipital
sq	squamosal
st	"sella turcica"
tc	trabecula communis
umf	unpaired medial fossa (= hypophyseal pit or unpaired cerebral carotid foramen)
v	vomer
vcl	vena capitis lateralis
II	optic nerve
V_1	endocast of the root of the ophthalmic branch of the trigeminal nerve (ophthalmicus profundus)
$V_{2,3}$	endocast of the roots of the maxillary and mandibular branches of the trigeminal nerve
VII_{pal}	presumed route of the palatine branch of the facialis nerve

MATERIALS

The following specimens form the basis for the present description of the braincase of *Placodus*:

- specimen BT 13 from the Oberfränkisches Erdgeschichtliches Museum in Bayreuth, acid prepared skull without the mandible (Sues, 1987, figs. 1-2; Pinna, 1989, figs. 1-2; Nosotti & Pinna, 1993, fig. 1; Rieppel, 1995, figs. 18-20, 23, 27A, 36A; Rieppel, 2000, fig. 14);
- specimen SMF R 4038 from the Senckenberg Museum in Frankfurt a.M., skull fragment with partial natural endocast of the braincase (otic capsule region), without the mandible (Edinger, 1928, pl. 24, fig. 1; Hopson, 1979, fig. 25);
- specimen SMF R 359 from the Senckenberg Museum in Frankfurt a.M., skull with the supraoccipital and parietal cut off, without the mandible (Broili, 1912, pl. 24, figs. 5-7), and plaster cast of the endocranium (Edinger, 1928, pl. 24, fig. 2; Hopson, 1979, fig. 25).
- specimen SMF R 1035 from the Senckenberg Museum in Frankfurt a.M., complete skeleton (Drevermann, 1933; skull in pls. 1-2). Available to us as a cast.

THE BRAINCASE OF *PLACODUS*

(Figs. 1 - 14)

The skull of *Placodus* is a solid, well ossified (partially pachyostotic), akinetic structure as is the case in all placodonts. The braincase is plesiomorphic relative to cyamodontoids in that it comprises the neurocranium ossifications and the associated dermal elements: the epipterygoid is not incorporated into the ossified lateral wall of the braincase as is the case in cyamodontoid placodonts (Nosotti & Pinna, 1996). The broad base of the epipterygoid of *Placodus* rests on the dorsolateral aspect of the pterygoid and the palatine. Dorsally, the epipterygoid abuts against the prootic, and anteromedially it contacts an ascending process of the palatine (Broili, 1912). Therefore in *Placodus*, unlike the cyamodontoid placodonts, the cavum epiptericum remains an extra-cranial space, the plesiomorphic condition.

In addition, an unpaired ossification forms an ossified bridge above the clinoid processes of the basisphenoid, referred to as the "alisphenoid bridge" by Broili (1912: 153). This structure, which is absent in the plesiomorphic reptile skull, is discussed in detail below (see page 9).

Description of the braincase

The otic-occipital region of the braincase of *Placodus* is fully ossified, forming a complete bony capsule enclosing the hindbrain and the labyrinth organ. It comprises the endochondral ossifications of the neurocranium normally expected in the plesiomorphic tetrapod skull, i.e., the basioccipital, the supraoccipital, the paired exoccipitals, the prootics and the opisthotics. The basisphenoid ossifies below the sphenoid region of the neurocranium: the dermal parasphenoid is intimately associated with the basisphenoid in the basicranium, so that these two bones are commonly referred to as the para-basisphenoid (or basisphenoid-parasphenoid complex).

The occipital region of the braincase, best preserved in the skull BT 13, has already been thoroughly described (Broili, 1912; Sues, 1987; Zanon, 1989; Nosotti & Pinna 1993 and 1996; Rieppel, 1995). Comparison with specimens SMF R 4038 and SMF R 359 confirms the presence of a well defined jugular foramen located between the exoccipital and the opisthotic and probably transmitting nerves IX, X and XI (and perhaps a root of nerve XII), and of a lower, smaller foramen piercing the exoccipital and probably transmitting nerve XII (Figs. 5A, B and 7).

In the otic region of the braincase, a large key-hole shaped fenestra vestibuli, located between the opisthotic, the prootic and the basioccipital, opens in front of the above mentioned foramina in BT 13 (Figs. 5A, B and 7). Specimen SMF R 1035, which was available to us as a cast, preserves the stapes *in situ*, corroborating our identification of the fenestra vestibuli in BT 13. The shaft of the stapes extends posterolaterally as it passes below the paroccipital process, its distal end contacting the medial surface of the quadrate. In specimen SMF R 359 the left quadrate shows a distinct and elongated stapedial recess on its medial surface.

The lateral wall of the braincase in the otic region (Figs. 1A, B, 7 and 8A, B) is formed by the ossifications of the neurocranium, and is completed dorsally by the descending flange of the parietal. As can be seen in specimen BT 13, the prootic is a wide ossification contributing to a large extent to the formation of the lateral braincase wall. The bone is pierced by a large prootic fenestra, for the exit of the maxillary and the mandibular branches of the trigeminal nerve. The identification of this large opening as a prootic fenestra is confirmed by the partial natural endocast of the braincase preserved in specimen SMF R 4038 (Edinger, 1928, pl. 24, fig. 1a, b, c; Hopson, 1979, fig. 25; Figs. 9-10 in this paper). On that endocast the trigeminal complex is preserved in great detail. It shows the ophthalmicus profundus branching off the root of the trigeminal nerve before the maxillary and the mandibular branches separate. As it branched off, the ophthalmicus profundus would have immediately turned anteriorly, passing medial to the epipterygoid. The common trunk of the maxillary and mandibular branches would have extended laterally, corroborating the identification of the trigeminal foramen within the prootic (prootic fenestra) in BT 13. The location of the foramen indicates that the maxillary and mandibular branches would have entered the cavum epiptericum, and passed behind the epipterygoid to make their way downward and anteriorly, lateral to the epipterygoid.

A large opening dorsal to the prootic fenestra on the right side of specimen BT 13 was previously interpreted as the prootic fenestra (Nosotti & Pinna, 1996: 34-35; Figs. 7 and 8A in this paper), framed by the prootic, the presumed laterosphenoid and the descending flange of the parietal. In the light of a closer examination of specimen BT 13 and of the interpretation of the braincase as a whole, this opening is found to be located within the descending flange of the parietal only, and most likely represents an artifact due to preparation with acid. The bone that is exposed medial to the opening is not a laterosphenoid (Nosotti & Pinna, 1996), but the prootic.

There is no distinct evidence for the exit of nerve VII through separate foramen/foramina, and for its course. It is possible that the hyomandibular branch of nerve VII passed out of the endocranium together with nerve V, then turned backwards into the cranioquadrate passage. Unlike in cyamodontoid placodonts, the cranioquadrate passage in *Placodus* is completely open, because there is no fusion of the dermal palate (pterygoid) with a neomorph otic process of the squamosal (absent in *Placodus*) and with the prootic. The palatine branch of nerve VII possibly gained its exit together with the main trunk of nerve V through the prootic fenestra, and may have continued its way forward by passing below the akinetic basipterygoid "articulation" together with the internal carotid (Fig. 7), thereby retaining its plesiomorphic course ventral to the basicranium (Nosotti & Pinna, 1996: 35).

The sphenoid region of the braincase deserves special discussion, because its morphology is not uniform throughout the different specimens examined, which critically affects the interpretation of the braincase as a whole, and of the structure of the brain. We briefly describe the morphology of this area in the different specimens, and discuss its interpretation in the next section.

The basicranium of the braincase of *Placodus* is best preserved in the acid-prepared skull BT 13 (Figs. 11 and 14A). In the sphenoid region the para-basisphenoid almost exclusively forms the braincase floor, with a limited lateral contribution of the palatine. The basicranium forms a relatively low, broad and transversely oriented dorsum sellae in between the anterior parts of the otic capsules. Laterally, on either side, the dorsum sellae extends into vertically ascending clinoid processes, which with their posterolateral surface contact the anteromedial aspect of the prootics. The clinoid processes are pierced at their bases by a foramen that presumably transmitted nerve VI, which thus retains relations to the hypophyseal area of the braincase that are typical of the plesiomorphic tetrapod skull. The clinoid process forms the medial margin of the anterior opening of the cavum epiptericum (which itself is the anterior continuation of the cranioquadrate passage), which would have transmitted the lateral head vein (vena capitis lateralis) (Figs. 7 and 11). The same opening is bordered laterally by a process ascending from the dermal palate, which contacts the dorsal tip of the clinoid process dorsally. In specimen BT 13 this process appears to belong to the pterygoid (Rieppel, 1995: 19; Nosotti & Pinna, 1996: 35), because a lateral suture appears to separate the palatine from the pterygoid anterior and lateral to this ascending process. However, the skull SMF R 4038 (Fig. 9), shows unequivocally that this process is part of the palatine (as was recognized by Broili, 1912): on the left side of the skull, lacking the epipterygoid, the palatine-pterygoid suture is very distinct, and can be followed upward

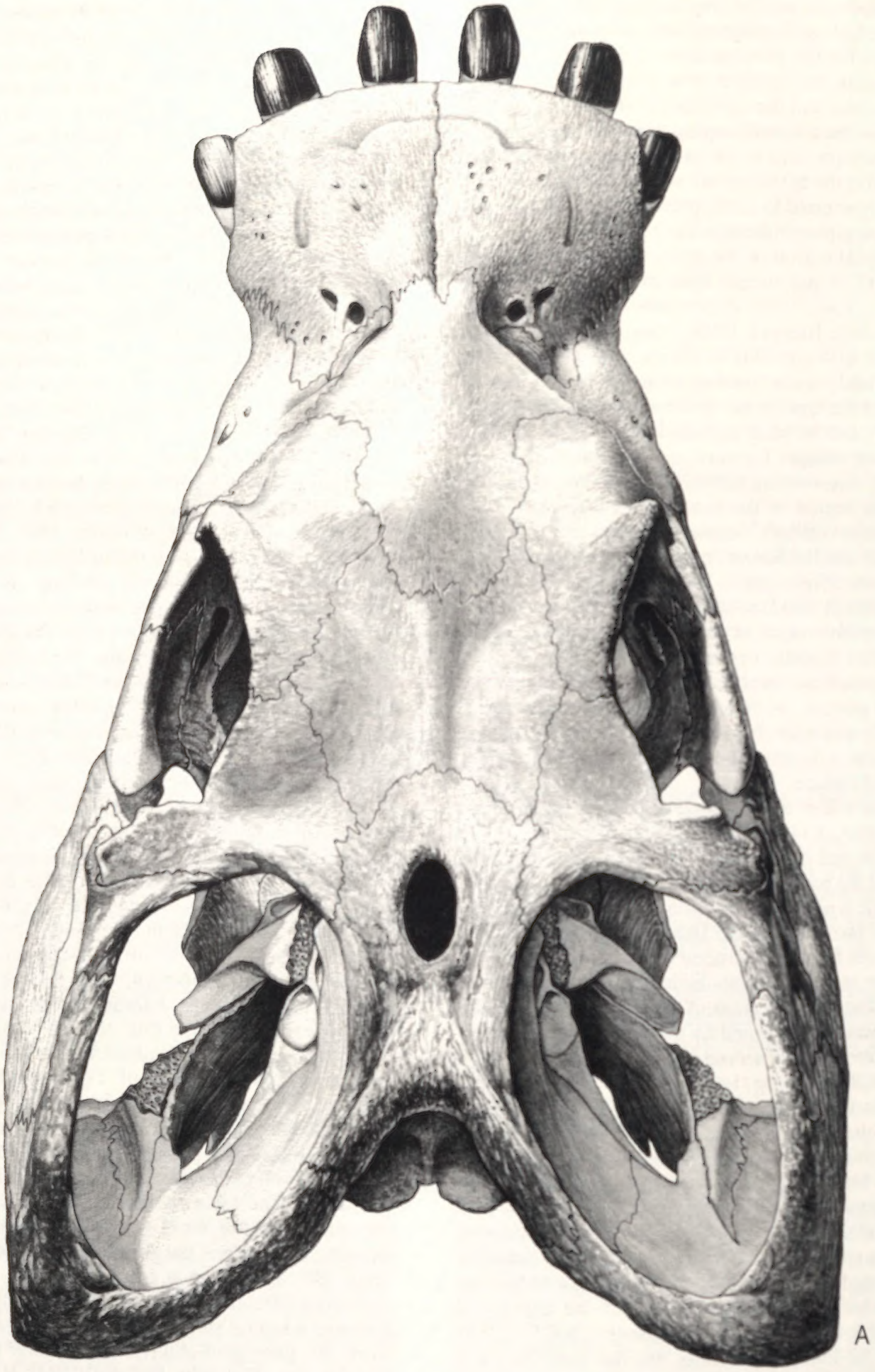
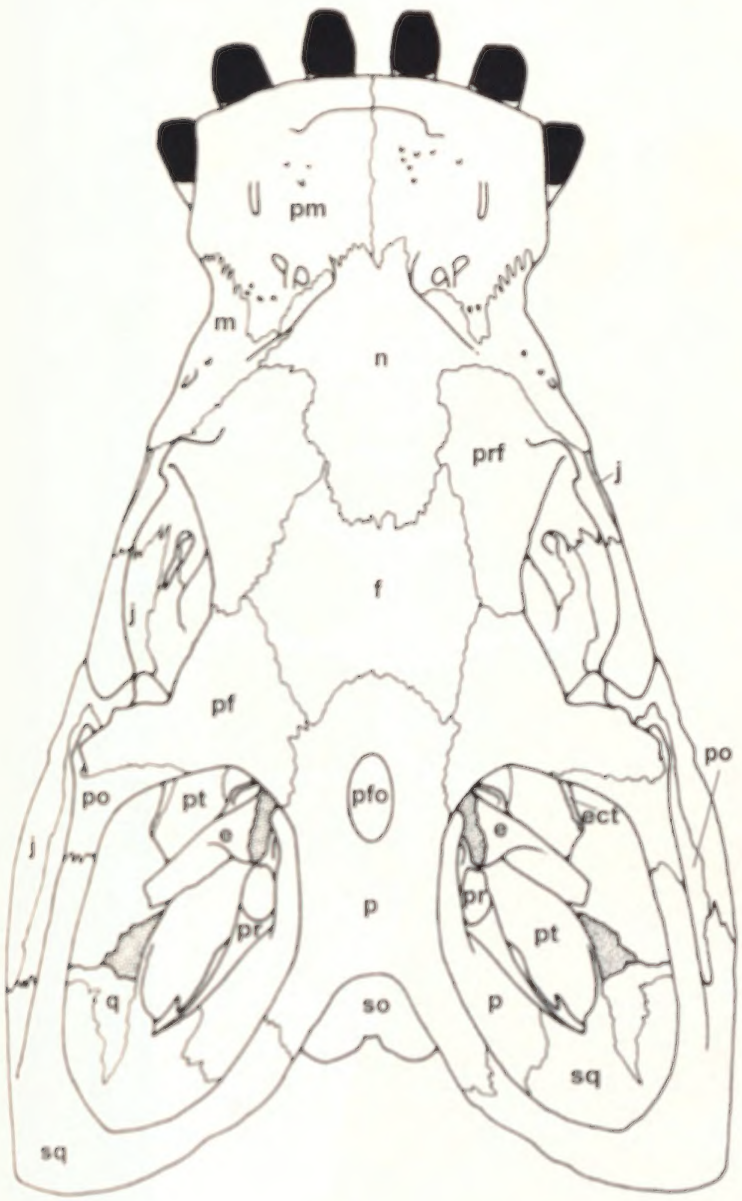


Fig. 1 A, B - Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Dorsal view. Drawings by Massimo Demma.



B

behind the ascending process. The continuation of this suture can be identified in the basicranium of specimen BT 13 as a weakly undulating line running forward medial to the ascending process (Fig. 11). The origin of this ascending process from the palatine is further corroborated by specimen SMF R 359 (Broili, 1912, pl. XIV, figs. 5-7). Therefore, we must conclude that BT 13 is misleading. Posteriorly, the ascending process of the palatine is applied to the the anteromedial margin of the epipterygoid.

A shallow, round medial fossa or depression is located on the dorsal surface of the basicranium well in front of the dorsum sellae, at the level where the para-basisphenoid becomes narrow to form a rostrum. For descriptive purposes, we will refer to this anterior medial fossa as the hypophyseal pit (see also discussion below). Two smaller foramina open on either side of this fossa, presumably transmitting the cerebral branches of the internal carotid arteries (here after referred to as the cerebral carotids), and two short and triangular, dorsally projecting processes are located between the medial fossa and the lateral foramina on either side (Figs. 11 and 14A). The putative hypophyseal pit is separated from the dorsum sellae by an elongated area, which forms most of the braincase floor in the sphenoid region. A distinct yet low ridge running along the midline of the dorsal surface of the basisphenoid extends between the dorsum sellae and the putative hypophyseal pit. In reptiles in general, the hypophyseal pit is located immediately in front of the dorsum sellae, which is not the case in the skull BT 13. The area which separates the putative hypophyseal pit from the dorsum sellae in the skull BT 13 is here referred to as "sella turcica".

In the skull SMF R 359 (Broili, 1912, pl. XIV, figs 5-7; Figs. 12B, 13 and 14B in this paper) the dorsal surface of the basicranium in the sphenoid region of the braincase has been completely exposed by removal of the parietal and supraoccipital. It closely resembles the morphology described for the skull BT 13, except for the absence of the ascending processes and of the foramina on either side of the anteriorly located hypophyseal pit described in the preceding paragraph. Instead, the unpaired medial fossa, i.e., the hypophyseal pit, is located closely in front of the dorsum sellae in the skull SMF R 359. In fact, the "sella turcica" is much shorter in the skull SMF R 359 than in the skull BT 13 (and not subdivided by a sagittal crest). Just as in specimen BT 13, the clinoid process in the skull SMF R 359 is pierced by a foramen that would have transmitted nerve VI, and it frames the anterior opening of the cavum epiptericum together with a process ascending from the dermal palate and formed by the palatine (Broili, 1912). Finally, specimen SMF R 359 is the only skull of *Placodus* that preserves the "alisphenoid bridge" (Broili, 1912, pl. XIV, figs. 5-7; Figs. 12B and 13 in this paper). This is a medial unpaired neurocranial ossification which transversely bridges the basicranium above the dorsum sellae area, fused to the medial surface of the anterior ends of the otic capsules (prootic) laterally and to the dorsal tips of the clinoid processes lateroventrally.

In the skull SMF R 4038, the dorsum sellae area is not very well preserved, even if distinct. Behind the para-basisphenoid rostrum this skull shows paired foramina in close juxtaposition to each other (Edinger, 1928, pl. 24, fig. 1a; in the present paper, Figs. 9, 10 and 14C). The latter foramina are more anteriorly located relative to the dorsum sellae if compared to the hypophyseal pit in SMF R 359, but less anteriorly located if compared to the paired cerebral carotid foramina in BT 13. They are not separated by an unpaired medial fossa (i.e., hypophyseal pit) as in specimen BT 13, and the ascending processes posterolateral to the presumed hypophyseal pit present in BT 13 are absent. Just as in the skull SMF R 359, the "sella turcica" of the skull SMF R 4038 is shorter than in the skull BT 13, and is not subdivided by a sagittal crest.

As far as can be judged from the three specimens examined, the lateral walls of the neurocranium in the sphenoid region of the braincase are not ossified in *Placodus* (but see Edinger, 1928: 312).

Finally, the sphenethmoidal region of the braincase of *Placodus* is peculiar because there is a high bony wall supporting the interorbital and nasal cartilagineous septa. This bony support is formed by the strongly raised and sutured medial parts of the palatines. Anatomical relations of the dermal ossifications enclosing the eyes, the olfactory tracts and the nasal capsules are shown in Figs. 1A, B - 6A, B.

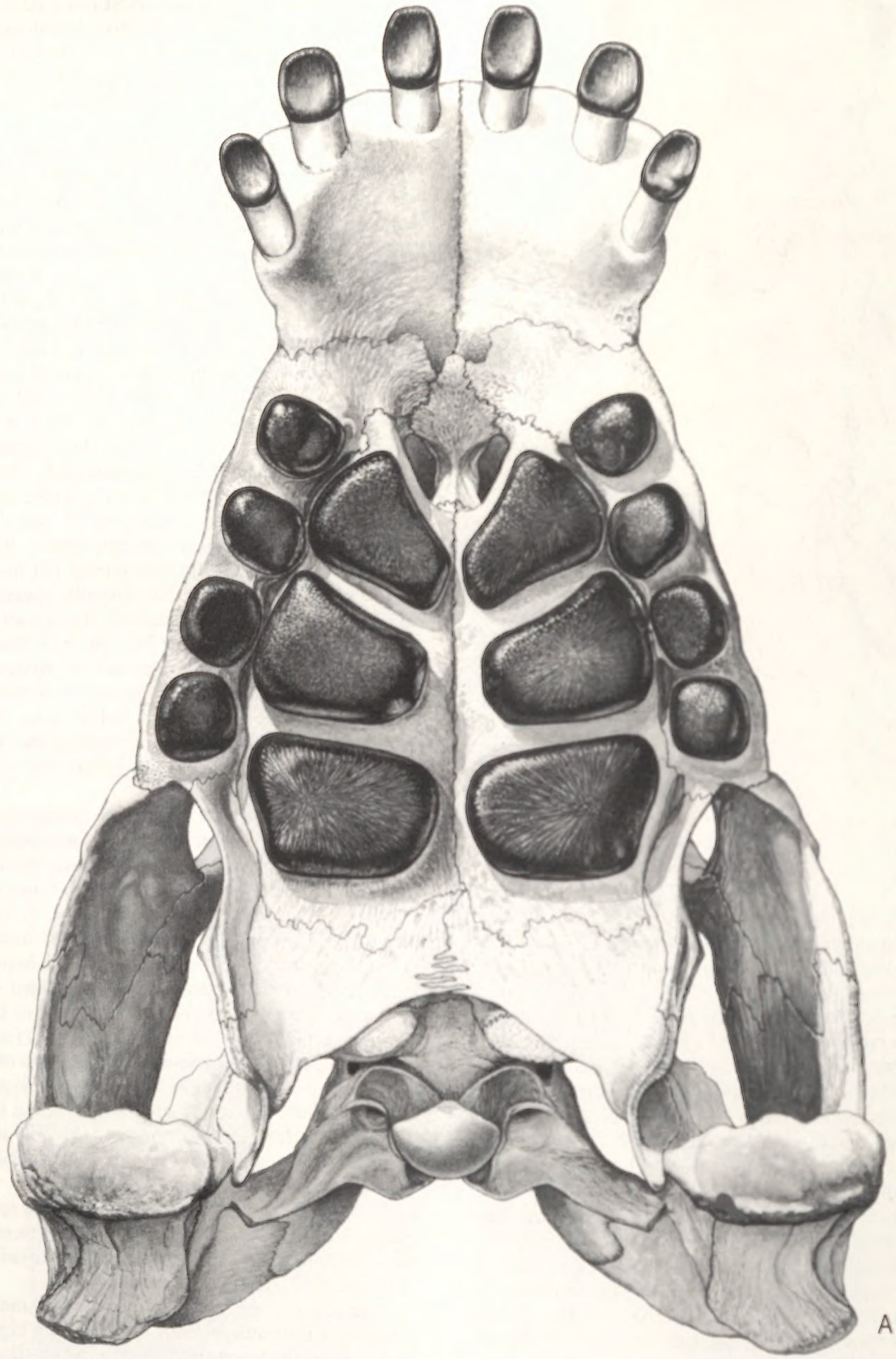
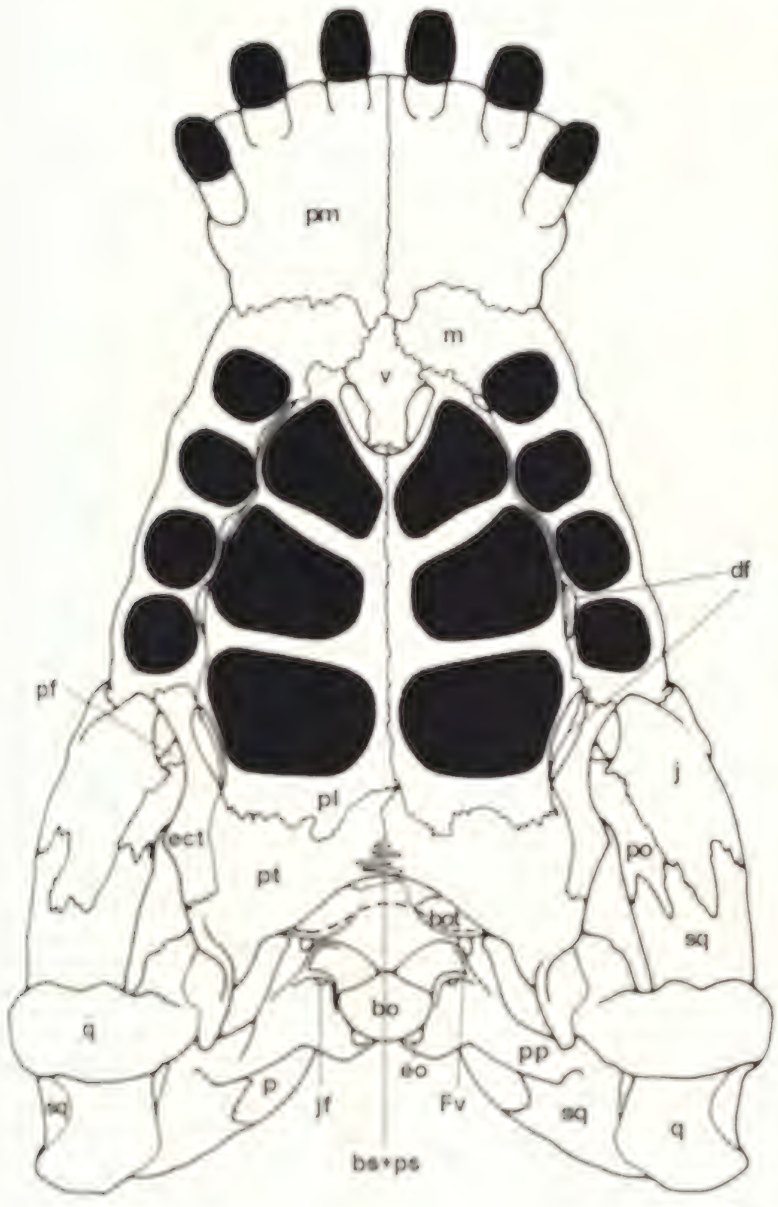


Fig. 2 A, B - Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Ventral view. The dashed line in Fig. 2B shows the presumed posterior margin of the pterygoids, which has not been reconstructed in Fig. 2A to expose the basioccipital tubera. Drawings by Massimo Demma.



B

The interpretation of the sphenoid region and of the "alisphenoid bridge" in the braincase of *Placodus*

In our view, a satisfactory interpretation of the sphenoid region of the *Placodus* skulls examined, the "alisphenoid bridge" included, can be attempted only by placing it in the context of an overall interpretation matching the structure of the braincase with the structure of the brain. The latter is indicated by the plaster cast of the endocranium in specimen SMF R 359 (Edinger, 1928, pl. 24, fig. 2a, b, c; this plaster cast of the endocranium of SMF R 359 is here after referred to as the "artificial" endocast, in order to distinguish it from the natural endocast preserved in SMF R 4038). Factors affecting our interpretation of the soft-part anatomy are the different morphologies of the basicranium throughout the examined specimens (see description on pages 5 and 7), and the topographical relationships of the "alisphenoid bridge" relative to the structures of the basicranium and of the brain. The latter has been differently reconstructed on the basis of the artificial endocast of the skull SMF R 359 by Edinger (1928, fig. B), and by Hopson (1979, fig. 25). As a consequence, we were unable to arrive at a conclusive assessment of the primary homology (*sensu* de Pinna, 1991) of the "alisphenoid bridge", the precise nature of which remains unknown.

Jaekel (1943: 46) was the first to relate the sphenoid region in the skull of *Placodus* to the soft-part anatomy. He interpreted an oval opening in the basisphenoid as the hypophyseal pit. Jaekel himself did not specify on which specimen he based his interpretation. However, as far as can be deduced from Edinger's comments (1928: 316), Jaekel's interpretation was based on specimen SMF R 359. This specimen shows the opening that Jaekel interpreted as the hypophyseal pit to be filled with matrix. On Jaekel's interpretation we found it impossible to identify the foramina for the entry of the cerebral carotids in that same specimen. Furthermore, because the putative hypophyseal pit is located in front of the dorsum sellae and of the "alisphenoid bridge", it must be concluded that on the basis of Jaekel's interpretation, the "alisphenoid bridge" would lie behind the infundibulum, and behind the hypophysis within the plica ventralis of the brain (Fig. 15A).

Edinger (1928) reconsidered Jaekel's interpretation of specimen SMF R 359 in the light of a second skull, i.e., specimen SMF R 4038. In this latter skull, paired cerebral carotid foramina can be identified some distance in front of the dorsum sellae (Edinger, 1928, pl. 24, Fig. 1a, "F.c.i."). In the same specimen, however, no unpaired medial hypophyseal pit is evident. In the light of specimen SMF R 4038, Edinger concluded that the opening referred to as the "hypophyseal pit" by Jaekel in specimen SMF R 359 was in fact the unpaired (i.e., fused) cerebral carotid foramen. Given this interpretation, Edinger was unable to identify an hypophyseal pit in either of those two skulls and hence declined to comment on the structure of the hypophysis in *Placodus*.

In the light of Edinger's interpretation of the basicranium of *Placodus*, the "alisphenoid bridge" may be assumed to have been located below the optic nerve root, how it was reconstructed by Edinger (1928, fig. B), but in front of the infundibulum (Fig. 15B). The artificial endocast does not indicate the infundibulum and/or the hypophysis attached to it, which may have added to Edinger's reluctance to comment on these structures. By contrast, she realized that if the "alisphenoid bridge" was located entirely in front of the brain, the infundibulum and the hypophysis would have had to be very small.

With the location in front of the brain, the "alisphenoid bridge" of *Placodus* could be compared to the laterosphenoid of crocodilians (Nosotti & Pinna, 1996: 34-35), which establishes a sutural contact anteroventral to the brain, incompletely flooring the forebrain. The laterosphenoids of crocodilians meet each other in front and above the hypophysis, and extend downwards and backwards lateral to the infundibulum and to the hypophyseal pit to meet the prootic along the margin of the trigeminal foramen. However, on the basis of Edinger's interpretation, the "alisphenoid bridge" in *Placodus* would lie below the optic nerve roots, whereas the anteromedial contact between the laterosphenoids of crocodilians is described to lie above the exit of the optic nerve (Iordansky, 1973). Finally the "alisphenoid bridge" of *Placodus* is a single structure, that would have to indicate fusion if we interpret it as the equivalent of the laterosphenoid in crocodilians.

Fig. 3 A, B – Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Lateral view. Drawings by Massimo Demma

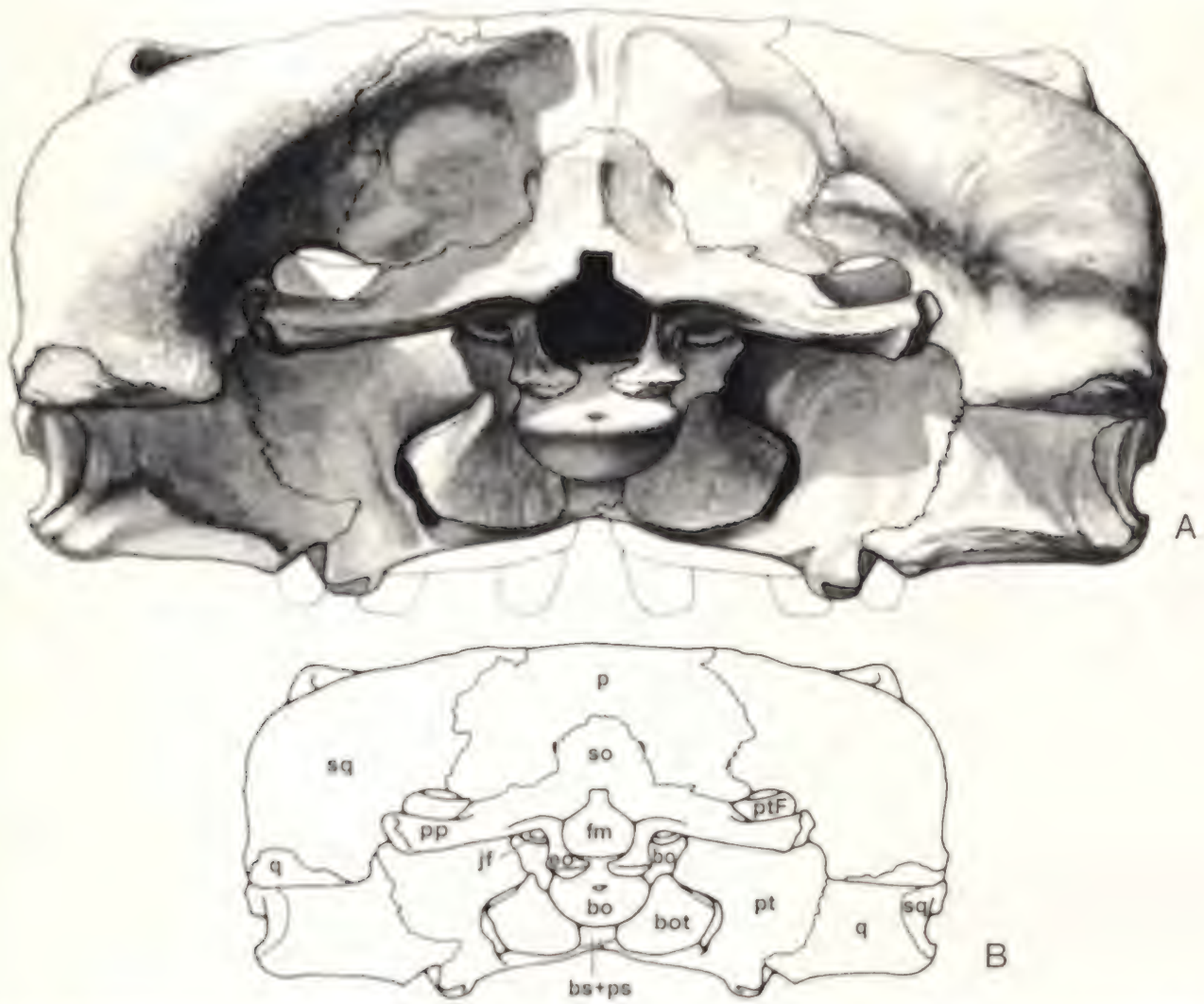


Fig. 4 A, B - Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Occipital view. Drawings by Massimo Demma.

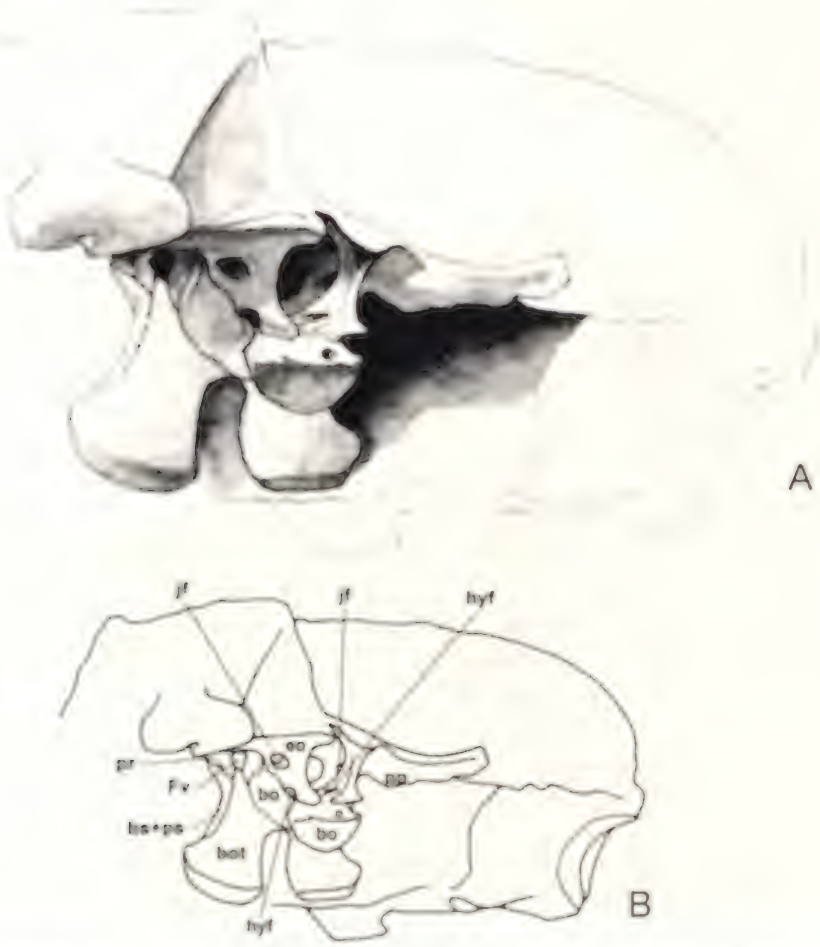


Fig. 5 A, B - Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Detail of the occiput in posterolateral view. Drawings by Massimo Demma

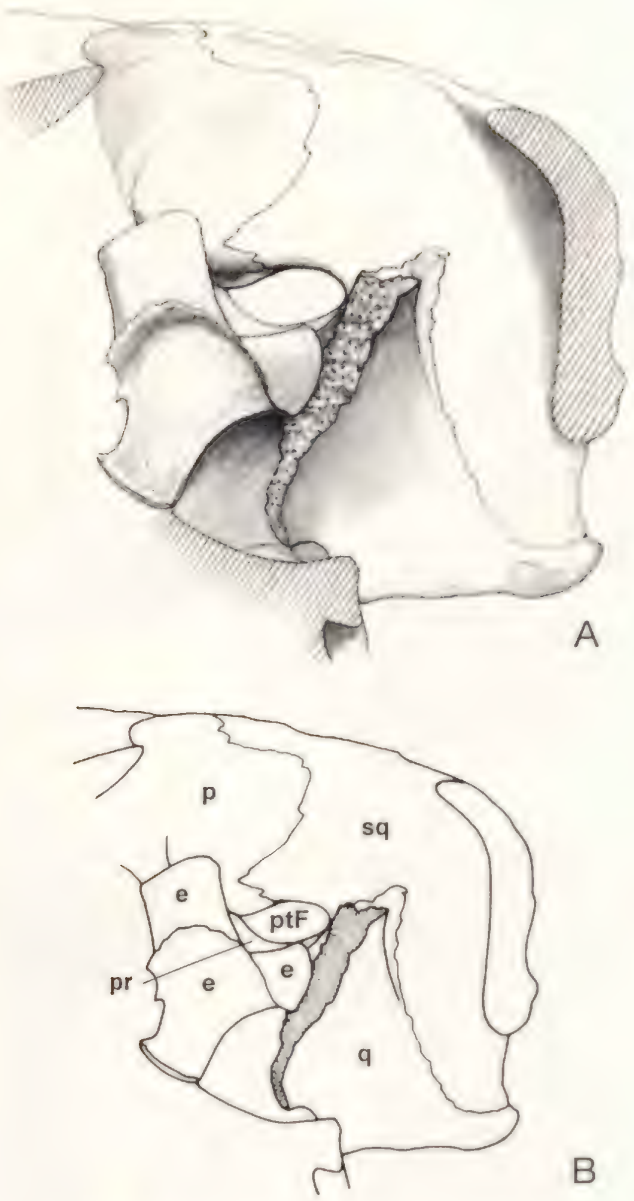


Fig. 6 A, B - Reconstruction of the skull of *Placodus*, chiefly based on specimen BT 13. Posterior aspect of the left temporal fossa in anterior view. Drawings by Massimo Demma.

In his review of Jaekel's and Edinger's interpretations of specimens SMF R 359 and SMF R 4058, Hopson (1979: 122-123) found that "*No remnant of the pituitary fossa is preserved on either endocast* [partial natural endocast of SMF R 4038, and artificial endocast of SMF R 359], *and Edinger omits it from her reconstruction of the brain. Its position and size can be restored on the basis of the figured braincase (Edinger, 1925, fig. 1A* [skull SMF R 4038]*). The dorsum sellae* [in the braincase of *Placodus*] *is high and steeply sloping, and the internal carotid foramina open on to the dorsal surface of the basisphenoid (i.e. the floor of the pituitary fossa) at about the same horizontal level of the ventral surface of the medulla. These features indicate that the pituitary fossa was large, but in the absence of bony anterior and lateral walls, its exact size cannot be determined*". It is clear that Hopson based his interpretation on the skull SMF R 4038 as figured by Edinger (1928, pl. 24, fig. 1a), apparently assuming that the structure labeled "Asph" was the steeply sloping dorsum sellae. In fact, that structure is the clinoid process of the basisphenoid. The area immediately in front of the dorsum sellae was interpreted by Hopson as the pituitary fossa, into which open paired cerebral carotid foramina. Hopson neither mentioned nor interpreted the unpaired medial fossa in specimen SMF R 359. However, in Hopson's figure 25, a composite endocast is shown, based on the artificial endocast of SMF R 359 with details added from the partial natural endocast of SMF R 4038. If the "alisphenoid bridge" is added to Hopson's figure, in the position relative to the artificial endocast that we verified on the original specimen (Fig. 15A), it is clear that the position of the pituitary fossa as restored by Hopson corresponds to the position of the unpaired medial fossa in SMF R 359. A corollary of Hopson's reconstruction of the pituitary fossa in figure 25 is that the unpaired medial fossa in SMF R 359 is the hypophyseal pit, as stated by Jaekel (1903). Hopson did not discuss this point however, and did not comment upon Edinger's

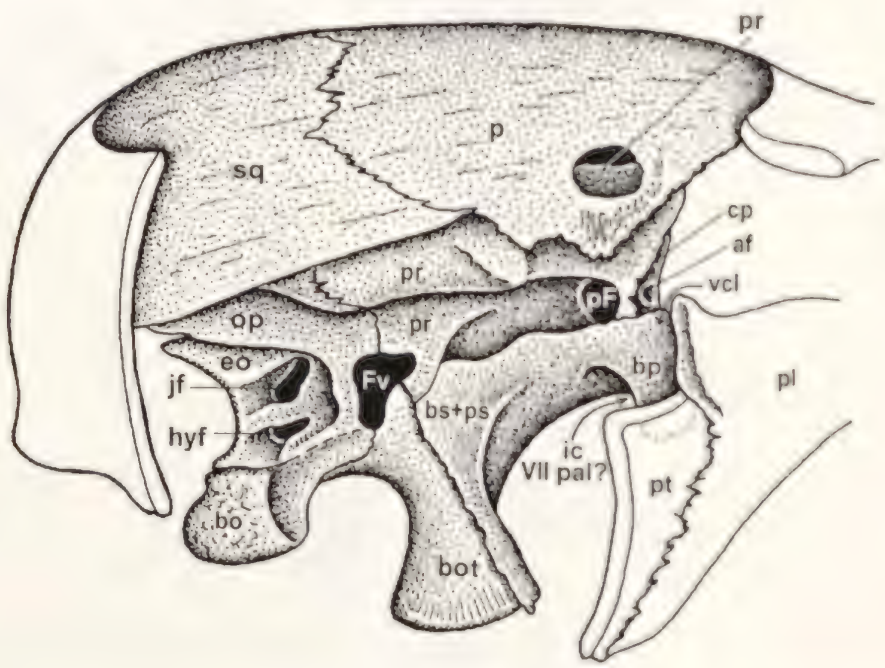


Fig. 7 - Lateral wall of the braincase of *Placodus* skull BT 13. The unfinished surface of the parietal above the prootic fenestra is the area where it abuts the dorsal end of the epipterygoid. Drawing by Olivier Rieppel.

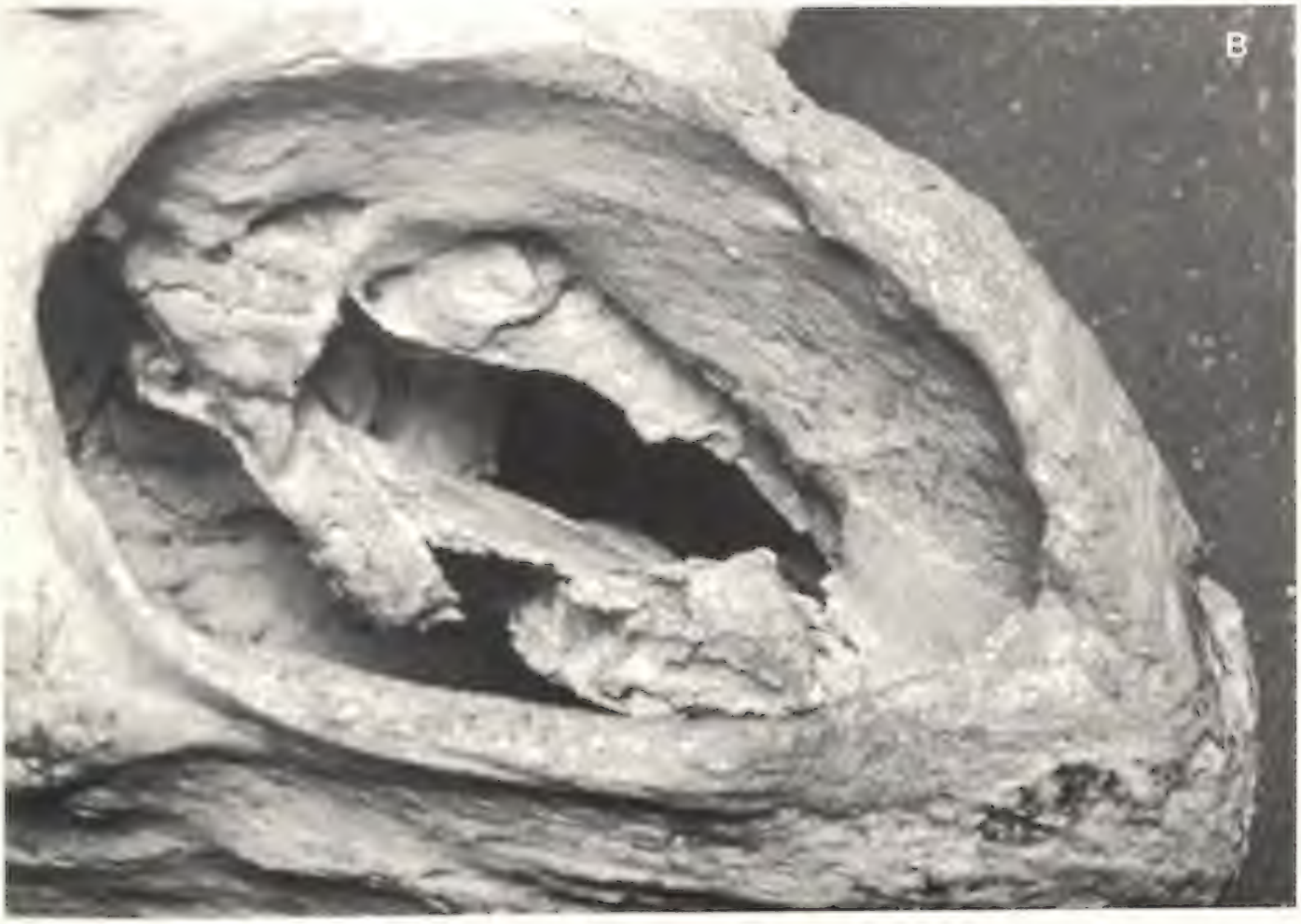


Fig. 8 A, B - (A) Right and (B) left temporal fossa of *Placodus* skull BT 13. The opening indicated by the arrow in (A) is an artifact. Photo by Luciano Spezia.

interpretation of the medial fossa in SMF R 359 as an unpaired cerebral carotid foramen.

The only skull of *Placodus* that shows the presence of an anteromedial depression that can be interpreted as hypophyseal pit in conjunction with paired cerebral carotid foramina is specimen BT 13 (Fig. 11), the neurocranium of which is here described in detail and interpreted for the first time. The anteromedial depression interpreted as the hypophyseal pit lies unusually far in front of the dorsum sellae. Likewise, the two cerebral carotid foramina are unusual in that they lie between the palatines and the basisphenoid. The incompletely ossified area in front of the hypophyseal pit might represent the area of the cartilago hypochiasmatica (de Beer, 1937). The nature of the two small processes rising up at the posterolateral corners of the hypophyseal pit in BT 13 remains unknown. For reasons of conjunction (Patterson, 1982), they cannot represent the clinoid processes, which are instead identified by their proper relationship to the dorsum sellae; likewise, they cannot represent the level of the primary lateral wall of the braincase, because they are located medial to the cerebral carotid foramina.

This interpretation of the skull BT 13 is in agreement with Jaekel in that it identifies a medial hypophyseal pit, but it adds to Jaekel's interpretation the paired cerebral carotid foramina. In contrast, specimen BT 13 refutes Edinger's assumption of an unpaired cerebral carotid foramen, because acid preparation documents the absence of such a foramen. The same cannot be unequivocally assessed in specimen SMF R 359 where the putative pituitary fossa *sensu* Jaekel is still filled with matrix.

The corollary of the interpretation of the unpaired medial fossa in the braincase of *Placodus* as an hypophyseal pit, is that the "alisphenoid bridge" is more probably an unpaired ossification of the neurocranium lying in the plica ventralis, posteroventral to the infundibulum, in agreement with Hopson's reconstruction of the brain (1979, fig. 25; Fig.15A in this paper). In fact, the hypophyseal pit of *Placodus* is located anterior relative to the position of the "alisphenoid bridge" (or its presumed position where it is not preserved). Most importantly, as a consequence of the interpretation of the "alisphenoid bridge" given above, it would represent a neomorph structure (Rieppel, 1995) not comparable to anything known in any other vertebrate.

An unresolved problem is the proportions exhibited by the basicranium of specimen BT 13. As described above, the hypophyseal pit and the cerebral carotid foramina are located in a far forward position, well in front of the dorsum sellae. With the "alisphenoid bridge" located in the plica ventralis, the low dorsum sellae remains separated from the hypophyseal pit by an extended "sella turcica", and the infundibulum as well as the hypophysis must be assumed to have extended anteriorly in a way unknown for all other reptiles. Also it is not clear which structure of the brain would have been accommodated by the very much and strangely elongated "sella turcica". The same problem does not apply to specimens SMF R 359 and SMF R 4058, but in these specimens the basicranium is less well preserved, because the foramina for the cerebral branches of the internal carotid and the hypophyseal pit are not identifiable in conjunction.

Fig. 9 - *Placodus* skull SMF R 4038 in left lateral view. The arrow points to the pterygoid-palatine suture. Photo by Olivier Rieppel.

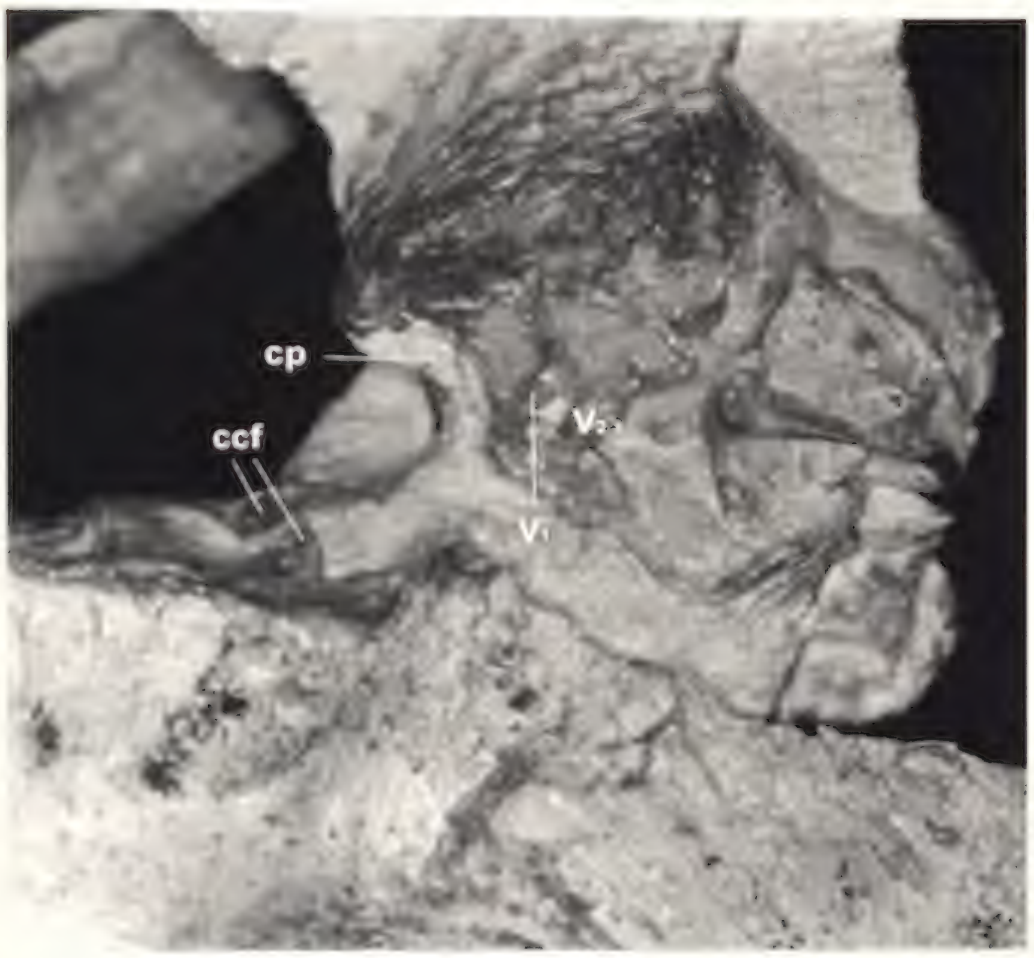


Fig. 10. Detail of *Placodus* skull SMF R 4038 in left lateral view showing the natural endocast of the left otic capsule. Photo by Olivier Rieppel

DISCUSSION

On the basis of the currently available material, no satisfactory overall interpretation of the braincase of *Placodus* can be arrived at. The occiput, the otic capsules, the topographical relationships of the epipterygoid and of the stapes, as well as the structure of the cranioquadrate passage and cavum epiptericum can all be satisfactorily analyzed and described in detail. The exact passage of the hyomandibular and palatine branches of nerve VII remains unknown, and the peculiar position of the trigeminal foramen fully within the prootic has been noted. The area more difficult to understand is the dorsal surface of the basicranium, and the identity of the structure described as the "alisphenoid bridge" by Broili (1912).

In the basicranium, the dorsum sellae is easily identified by its relationship to the clinoid processes and the foramina for the passage of nerve VI. In reptiles in general, the sella turcica is located closely in front of the dorsum sellae. The "sella turcica" appears very elongated in *Placodus* (skull BT 13), and subdivided by a longitudinally oriented ridge on the dorsal surface of the basisphenoid. This ridge widens as it approaches a shallow medial depression narrowly behind the para-basisphenoid rostrum, with small dorsal projections located posterolateral to that depression. If that depression is interpreted as the hypophyseal pit (Jaekel, 1903), the latter would be in an unusual location, far in front of the dorsum sellae, and the structure described as the "alisphenoid bridge" would come to lie in the plica ventralis of the brain.

Conversely, Edinger (1928) interpreted the skull SMF R 359 as showing a single foramen for the entry of the cerebral carotids into the braincase. An unpaired medial opening for the entry of both cerebral carotids is a condition unknown in any other vertebrate. Moreover, the skull BT 13 (prepared with acid) documents the absence of an unpaired medial cerebral carotid foramen. Rather, each cerebral carotid appears to have entered the braincase through a separate foramen. These foramina are located posterolateral to the hypophyseal pit in BT 13, enclosed by the para-basisphenoid and the palatine. In specimen SMF R 4058, the cerebral carotid foramina are located closer towards the dorsum sellae and closer towards the midline of the skull (Edinger, 1928, pl. 24, fig. 1a). Although the participation of the palatine in the lateral closure of the cerebral carotid foramen in BT 13 is unusual (and possibly autapomorphic for *Placodus*), the cerebral carotids would have entered the braincase in a position relative to the hypophysis which is closely comparable to that of other reptiles (if it is assumed that the hypophysis is, indeed, located in the shallow anterior depression well in front of the dorsum sellae: Jaekel, 1903). In reptiles in general, the cerebral carotids enter the basicranium near the hypophysis, which thus comes to lie in the centre of the circle of Willis formed by the anterior and posterior branches of the cerebral carotids. It re-

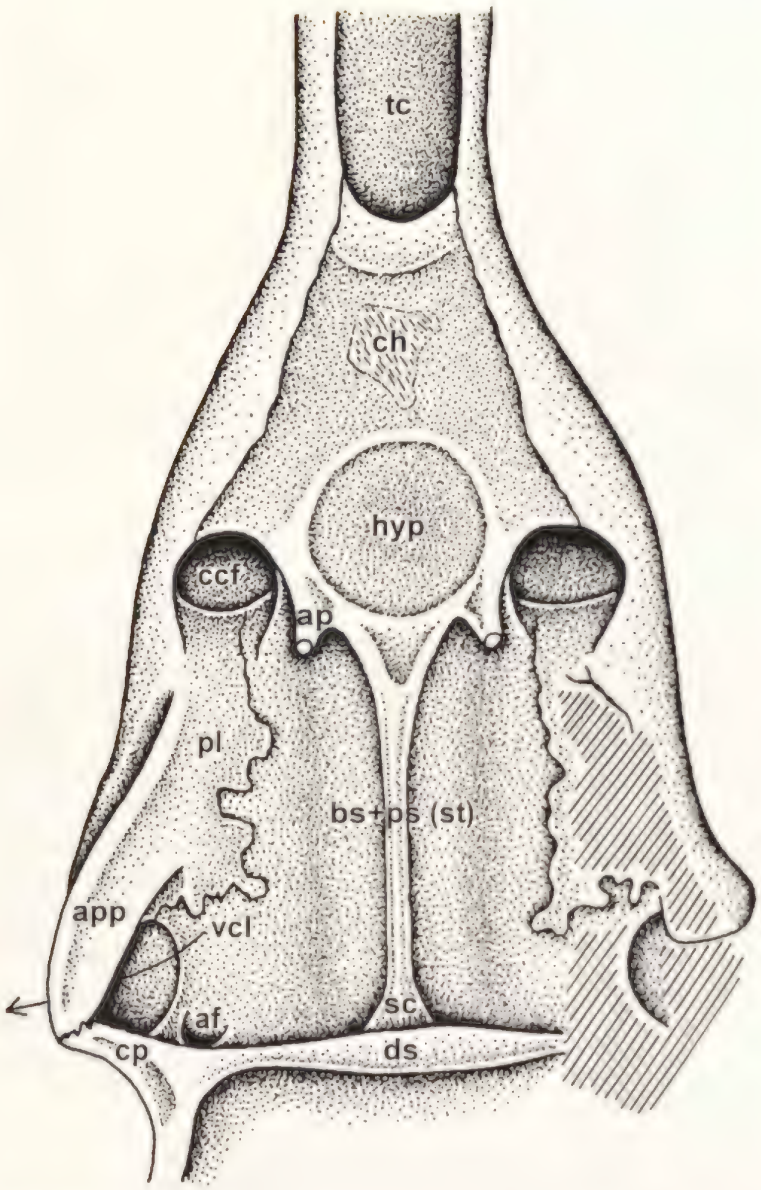


Fig. 11 - Basicranium of *Placodus* skull BT 13. Dorsal view. Drawing by Olivier Rieppel.

mains unclear what structure was accommodated by the elongated "sella turcica" in the skull BT 13.

The skull BT 13 shows small, dorsally projecting processes posterolateral to the putative hypophyseal pit. For reasons of conjunction (Patterson, 1982), these cannot represent the clinoid processes. It seems that these processes, therefore, are again neomorphs, possibly an autapomorphy of *Placodus*. In reptiles in general, the hypophysis is located closely in front of the dorsum sellae, and behind it the retractor bulbi muscles originate from the retractor pits in the dorsum sellae (Säve-Söderbergh, 1946). Given the far anterior position of the hypophyseal pit in the skull BT 13, it would seem possible that the dorsally projecting processes located posterolateral to it served as the site of origin of the retractor bulbi.

Of the two possible interpretations of the braincase of *Placodus* outlined in the descriptive section above, the position of the "alisphenoid bridge" in the plica ventralis appears to be the more plausible alternative (see also Hopson, 1979, fig. 25), because it perhaps creates less problems in fitting the proportions of the brain (as indicated by the artificial endocast) to the braincase itself. In essence, however, both interpretations of the "alisphenoid bridge" must remain highly conjectural, because each creates its own topographical problems in the interpretation of the basicranium, and of the relation of the brain to the braincase. The case has frequently been made that topographical relations provide a "test of similarity" for primary conjectures of homology (e.g. Patterson, 1982). But it has also been recognized that the application of topographical criteria in a "test of similarity" requires a frame of reference which, for the instance of that particular comparison, has to be held constant (Rieppel, 1988). This, however, is unproblematic as long as this frame of reference can in itself be critically evaluated. However, the braincase of *Placodus* provides a prime example of a complex structure for

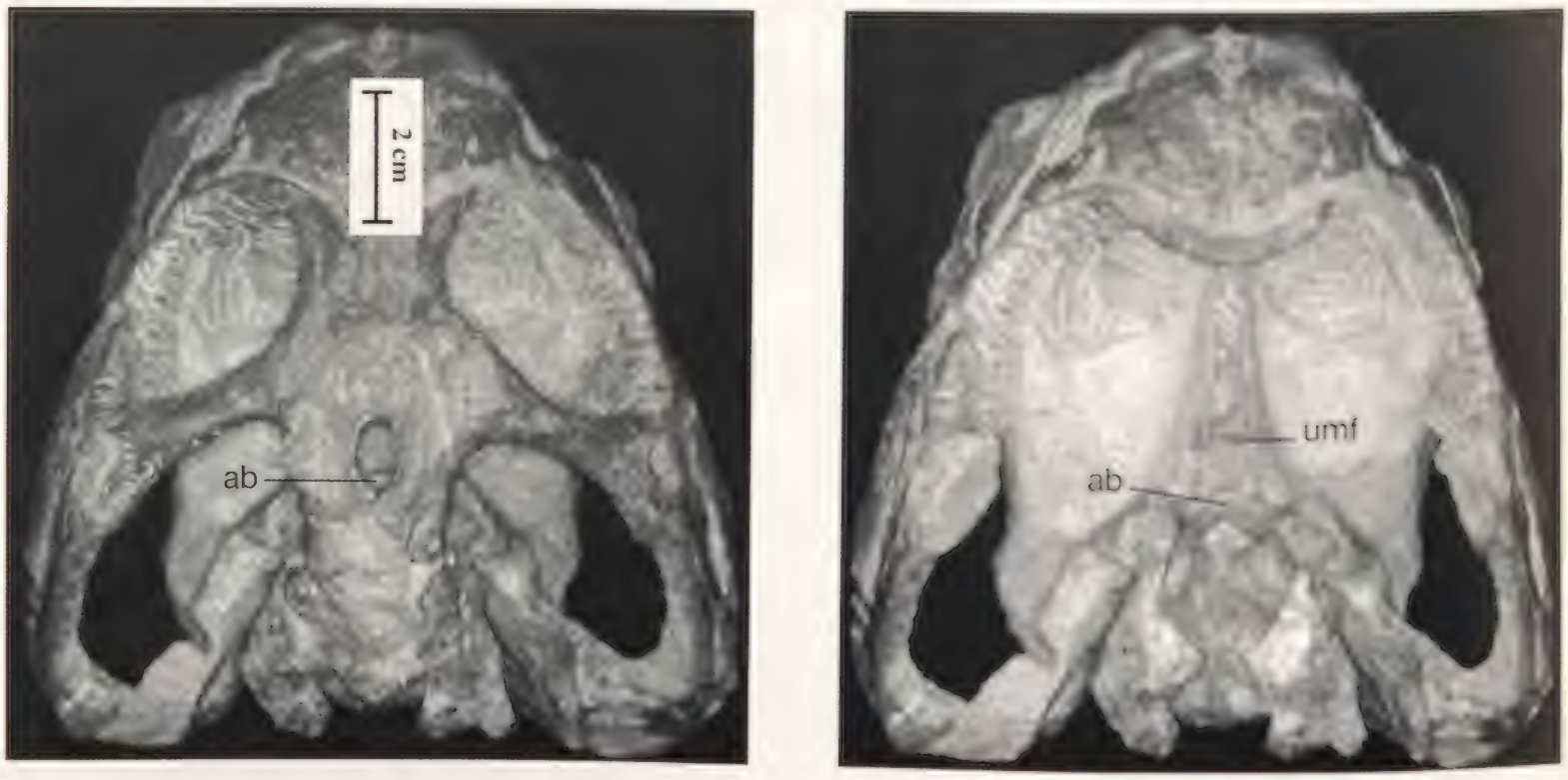


Fig. 12 A, B - *Placodus* skull SMF R 359 in dorsal view. (A) with the skull roof complete; (B) with the supraoccipital and the parietal cut off. Photo by Olivier Rieppel.

Fig. 13 - Detail of the neurocranium of *Placodus* skull SMF R 359. Photo by Olivier Rieppel.

which there is no closely comparable extant model on which to base a morphological interpretation. All that can be done in the interpretation of the basicranium and of the "alisphenoid bridge" in *Placodus* is to start out with a certain basic assumption, which establishes a frame of reference, and hence provides a basis from which to infer the morphological interpretation of the whole complex. In the case of *Placodus*, two alternative basic assumptions have been made historically (Jaekel, 1903; Edinger, 1928), none of which is unproblematic in itself (in terms of topographical relations), and each of which results in a radically different interpretation not only of the basicranium, but also of the "alisphenoid bridge" and its relation to the brain.

Acknowledgements

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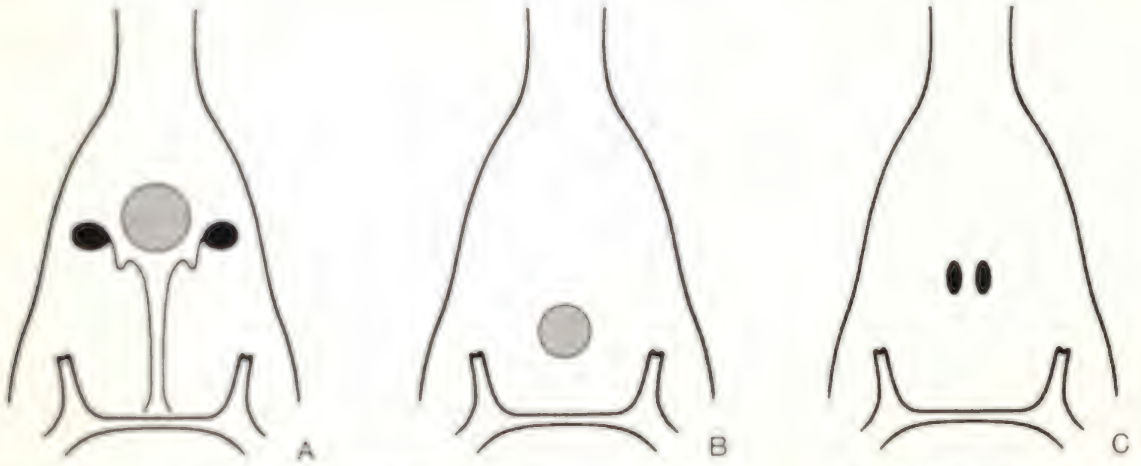

Fig. 14 - Schematic drawings of the basicranium in *Placodus* specimens (A) BT 13, (B) SMF R 359, (C) SMF R 4038. Sketch by Massimo Demma.

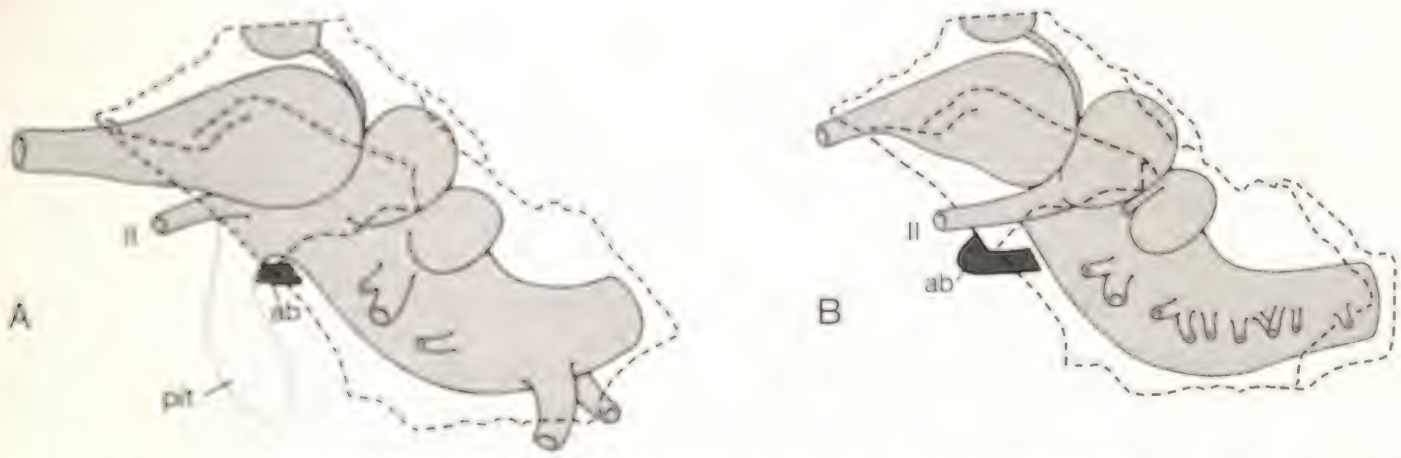

Fig. 15 A, B - Reconstruction of the brain of *Placodus* drawn against the artificial cast of the endocranium (broken line) obtained in specimen SMF R 359 (Edinger, 1928, pl. 24, fig 2a). (A) partially redrawn from Hopson (1979, fig. 25) and completed; (B) redrawn from Edinger (1928, fig. B). The "alisphenoid bridge" is drawn in the position relative to the artificial cast that we personally observed. Drawings by Massimo Demma.

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